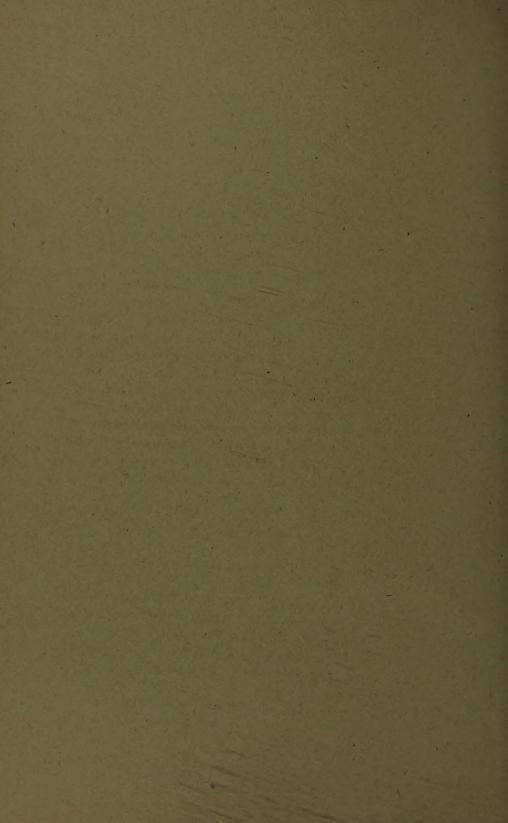
# STUDIES IN THE GENUS GYMNOSPORANGIUM-II.

# REPORT ON CULTURES MADE IN 1915 AND 1916



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# Studies in the genus Gymnosporangium—II. Report on cultures made in 1915 and 1916

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(WITH PLATE 8)

The writer (2) reported the infection of Chamaecyparis with Roestelia transformans, and later (3) gave an account of experiments which resulted in the infection of the red cedar with G. clavipes, G. macropus, G. globosum and G. nidus-avis. Arthur's results (1) were confirmed in the case of G. clavipes, and it was stated that the other species required nearly two years to mature. G. globosum as well as G. macropus may develop strictly foliicolous galls. In 1917 the writer reported the infection of Chamaecyparis with G. Ellisii (4). Weimer (12) states that G. clavipes matures in two years, although it seems he was unable to make the infections. He also reports the development of one small gall of G. macrobus on cedars which he had previously inoculated. The abstract of the writer's paper read at a meeting of the Botanical Society of America, 1916, has not appeared in print, and as further work has resulted in the accumulation of considerable data, a summary of the cultures of 1915 and 1916 is presented at this time.

#### GYMNOSPORANGIUM CLAVIPES

A red cedar eight inches high obtained from Cold Spring Harbor, Long Island, in May, 1915, had at the time a few sori of *G. clavipes* on the stem. This material was used to infect *Crataegus oxyacantha*.

Six red cedars were sprayed with aecidiospores August I, 1915, and left in the infection frame two days. Several other cedars were growing in the same greenhouse, otherwise no controls were provided. Table I includes all cedars that were growing in the greenhouse at the time aecidiospores were being shed from the rust on the *Crataegus*.

The results shown in the table indicate that spores may mature the first spring after inoculation, although in some cases they do not appear until the second year. All of the plants that were inoculated became so heavily infected that by 1918 many of the branches had been killed. Those plants that became infected without inoculation through being exposed near hawthorns bearing aecidia bore only a few sori in 1917 and had about twice as many in 1918. The invasion of new regions of the host by the mycelium

TABLE I

INOCULATION OF Juniperus virginiana WITH AECIDIOSPORES OF G. clavipes

	Plants inoculated Au	gust 1, 1915	Cedars exposed in the greenhouse but not inoculated by spraying, etc.			
No.	Results, 1916	Results, 1917	No.	Results, 1916	Results, 1917	
401		+, many sori	405		+, 6 sori	
402		+, " "	407	-	_	
403	-	+, " ".	408	-	_	
412	+, II sori	+, " "	411			
415	+, 30 sori	+, " "	938	-	_	
416	+, I sorus	+, " "	413	_	-	
			414	_	_	
			417	-		
			418	-	+, 2 sori	
			590	-1 7		
- 1			591	-	_	
			594	_	-	
			600		_	

is not very rapid. It has, however, completely connected spaces between most of the groups of sori that were evident on the plants in 1917. In some cases small witches' brooms have been formed, and spindle-shaped swellings are beginning to appear on some of the larger branches and main stems.

# Gymnosporangium macropus

The life histories of the two "cedar apple" rusts have become fairly well understood through field observations made by many investigators of the gymnosporangial stages, and by cultures of the rusts on their aecidial hosts.

The cedar plants used in this work were obtained at Cold Spring Harbor, New York, February 1, 1914. Some of them bore a few galls of *G. macropus* and *G. globosum*. Spores from these galls were used to infect seedling apples and hawthorns. The galls were marked with tags for further observation. The cedars were carefully inspected during the summer of 1914 and until

July 1, 1915, and any new galls that appeared were marked with tags. The heights of the plants were taken in February, 1914, and each spring since that date. These precautions enabled me to obtain evidence relating to the length of life of the galls, especially of G. globosum, which has been assumed to be perennial, although records bearing on this point appear to be meager. Hawthorns bearing aecidia of G. globosum were grown in the greenhouse at the same time and this fact required that infections be made with teleutospore material from galls that appeared on the cedars later, since the smaller galls of G. globosum and G. macropus are not always so characteristic as to be easily distinguished. The results are given in Table II.

TABLE II

INFECTION OF THE RED CEDAR WITH G. macropus

No.	Height of cedars, inches							
	Feb.,	Feb.,	Feb.,	Feb.,	Date of inoculation	Results, number of galls	Spores matured	
					1914			
401	II	16	24	38	July 13	0		
403	7	12	26	35	June 13	2	March 17, 1916	
504	6	IO.	15	23	June 7	. 3	March 6, 1916	
411	14	24	39	53	June 22	0		
414	16	24	39	53	June 20	2	May 18, 1916	
415	9	13	- ?	20	June 28	2	April 2, 1916	
417	16	21	34	48	June 20	0		
403	7	12	26	35	1915	3	April 14, 1917	
					July 2			
407	12	22	35	50	Aug. I	6	April 24, 1917	
416	.10	14	17	24	June 5	2	April 25, 1917	
418	?	?	20	42	June 10	I	March 1, 1917	

The last date upon which the plants were exposed to natural infection was in the summer of 1913. The point at which the lowest gall, for example on plant No. 403, appeared was five inches above the tip of the main stem of this plant February 1, 1914, as shown by the records of measurements. The cultures, especially those made in 1915, prove that Heald's conclusions were correct as regards the time required for the maturity of the rust. There were fourteen galls on these four plants; they were for the most part comparatively small, bearing from one to five sori.

#### GYMNOSPORANGIUM GLOBOSUM

The inoculations of cedars with *G. globosum* were made in 1914 and 1915 under the conditions described in the preceding experiments. The results appear in TABLE III.

TABLE III

INFECTION OF THE RED CEDAR WITH G. globosum

No.	Height of cedars in inches						
	Feb.,	Feb.,	Feb., 1916	Feb.,	Date of inoculation	Results, number of galls	Spores matured
					1914		
405	6	10	15	23	June 7	15	March 7, 1916
407	12	22	35	50	June 25	5	Feb. 28, 1916
408	II	20	30	48	June 20	0	1
					1915		
401	II	16	24	38	Aug. I	0	
402	14	3	26	37	Aug. I	. 0	
403	7	12	26	35	Aug. I	2	March 10, 1917
405	6	10	15	23	Aug. I	I	April 4, 1917
416	IO	14	17	24	Aug. I	0	

The first indications of infection were discovered August 1. 1915; there were two small green galls on plant No. 407. The writer is rather inclined to disregard these galls, especially as they were on the lower branches and grew to considerable size like those one finds in nature. There were no sorus-scars such as we should expect to see if the plants had been infected in nature in 1913. The other galls were clearly the result of inoculation as most of them developed at points on the plants represented by new growth since they had been brought in. None of the fifteen leaf galls on plant No. 405 developed sori a second time. The ones on No. 407 matured spores two seasons. Most of the large galls on naturally infected plants, so far as observed, bore sori three years in succession. There is no record of one bearing four crops of spores. It was impossible to inspect the cedars thoroughly during July and August, so that it is uncertain at just what time the galls made their first appearance. Most of them were visible in September, although some of the galls of G. globosum were so small that they might have been overlooked. In some cases there is very little hypertrophy of the leaf tissue upon which they appear. Weimer (II) has very adequately described these small galls.

### GYMNOSPORANGIUM ELLISII

Fromme (6) connected Gymnosporangium Ellisii with Aecidium myricatum. Dodge and Adams (5) found the aecidium on Comptonia asplenifolia. Attempts were made to infect Comptonia in 1915 and 1916 without success. The plants brought in March 25, 1917, leaved out in about two weeks and were inoculated April 12. The spermogonia appeared April 1 on several leaves. By May 14 the peculiar ram's horn twist of the leaves was very striking. Absence prevented further observation of the infected plants but at least two of them matured aecidia.

Certain seedling plants of *Chamaecyparis* were sprayed with aecidiospores from *Myrica* in 1915 and others in 1916. The cedars in the first lot showed no signs of infection in 1916, three years after they had been exposed to natural infection. The second lot consisted of small seedlings, one to three inches high. The results of these experiments are given in Table IV.

TABLE IV

Infection of Chamaecyparis thyoides with G. Ellisii

A. Inoculation, 1915

No.	Date of inocu- lation		Results		
		1916	1917	1918	Controls
345	June 21	_	+ 5 Infec.	+	Eighteen other plants were
349	June 21	-	-		exposed in the same greenhouse
400	June 21	1 -	+ 4 "	+	several weeks where aecidio
404	June 21	_	_		spores were being shed, but the
406	June 21	_	+ 2 "	+	were not sprayed and kept in
410	June 21	_	+ 1 "	+	moist chambers. Only one
420	June 21	-	+ 14 "	+	plant, No. 431, became infected
426	June 21	-	_	-	One sorus developed on young
433	June 21	-	+ 1 "	+	growth of a branch.
436	June 21	ense		-	

#### B. Inoculation, 1016 Eighty-four similar plants 906 April 24 were exposed, but not sprayed +++++ 907 April 24 in the infection frame. No in-008 April 24 fection has appeared on these April 28 plants. May 4 914 May 4 916 May 4 918 May 17 Plant died 953 June I June 1 954 June I June I 956 June I 957 June I 958

The table shows that eighteen of the twenty-four plants inoculated became infected, one of them in fourteen different places. Sori matured about twenty months after inoculation, except in the case of plants Nos. 907, 908, and 909, where sori developed the year following inoculation. It is possible that in some cases this species may mature in one year especially where inoculations are made as early as April 24.

In many cases there is but little hypertrophy or distortion of the leaves or twigs when the sori are first formed. There is a slight bending of the tip of the branch and a cushion-like swelling is developed beneath the sorus. After another year a witches'-broom of considerable size is formed, or if the main stem is infected a slight spindle-shaped swelling occurs. Sori may be foliicolous with the primordia in the leaf tissue, but in all cases the mycelium penetrates into the wood of the branch.

## Gymnosporangium clavariaeforme

The telial stage of G. clavariaeforme was obtained from New Haven, Connecticut, through the courtesy of Dr. Clinton and Dr. Nichols. Several plants of Amelanchier and other pomaceous hosts were inoculated May 9-13, 1916. The most abundant aecidia were produced on Amelanchier canadensis and A. intermedia. If spores are floated on water in damp chambers the percentage of germination is ordinarily about 95 per cent.

Five plants of *Juniperus communis* had been obtained from a nursery in New Jersey in 1915. They were about one foot high. Six smaller plants, three to six inches high, came from Glen, New Hampshire. Nine of these junipers were sprayed with spores in June, 1916. They were taken from the cold frame March 7, 1917. Two plants from New Hampshire were used as controls and showed no signs of being infected. Minute sori were discovered on three plants in April. No further inspection was made from May 14 until September 10. At this time slight swellings along the stems of two of the infected plants could be distinguished. Three of the nursery plants died before January 7, 1918. The results of these inoculations are given in Table V.

TABLE V

INFECTION OF Juniperus communis WITH G. clavariaeforme

, No.	Date of inoculation	Results noted March 7 to May 14, 1917	Results January 7, 1918
	1916		
925	June 10	Plant died 1916.	
926	June 6	No infection.	Plant died 1917.
931	June 6	One infection.	Two infections.
932	June 6	No signs of infection.	Plant died 1917.
933	June 6		One infection.
959	June 29	Two infections, lost many leaves.	Three infections.
960	June 29	No signs of infection.	One infection.
961	June 29	One infection.	Two infections.
962	June 29	No infection.	No infection.

There were nine separate infections in all. One of the plants from New Hampshire was not infected. The two control plants remained uninfected. Sections of three of the swollen stems were made January 17, 1918, ten days after the plants had been taken from the cold frame. It was found that teleutospores were being formed, although the sori had not yet broken through the bark. In sections even at the lowermost points of the swellings there appeared only two annual rings of wood. There were at first no signs of infection but minute sori with a few spores each developed on three of the plants during the last of April, 1917. The fact that sori formed the first year may be so small as not to break through the cork or epidermis, and therefore not be detected, should always be considered. Sections made the next year will show the cork callus at the point where the sorus was located. The infection of these plants undoubtedly occurred on the new growth of the spring of 1916. These cultures do not furnish much evidence that, as Plowright maintains (9), sori are not produced the spring following the year of infection. Tubeuf (10) gives a detailed and quite convincing account of his cultures of the species and there is no doubt that the incubation time may vary. This period does not appear to be absolutely fixed in the case of the infection of the red cedar with G. clavipes and G. Ellisii, which the writer has previously noted, and it will be shown later that the incubation time varies when cedars are infected with G. nidus-avis.

# GYMNOSPORANGINM JUVENESCENS

The telial stage of *G. juvenescens* was obtained from Dr. J. J. Davis, Madison, Wisconsin, in April, 1916. Sori were present in the axils of the acerose leaves, but the witches'-broom effect was not pronounced. Three or four plants of *Amelanchier intermedia* and *A. spicata* that were in bloom at this time were inoculated. Infection was evident in five days. Aecidia matured in abundance on fruit and leaves as early as May 1.

Nine red cedars were inoculated in 1916. No infection appears to have followed these inoculations; there are as yet, April, 1918, no indications of swellings or the development of sori.

#### Gymnosporangium nidus-avis

The red cedars on Long Island and in the vicinity of New York are badly infected with a *Gymnosporangium* which, if the infections are due to a single species, is certainly multiform in its manifestations. *Amelanchier* and *Malus* have been infected with spores taken from each of the following forms, although the inoculations were not made in each case with a single sorus: (1) Sori in the axils of densely crowded acerose leaves; (2) sori caulicolous, large branches forming coarse witches'-brooms; (3) trunk infections, sori appearing in deep fissures in the thickened bark. There is perhaps another form recognized by the presence of long parallel cork ridges, about one centimeter in width, that mark the location of sori of former years.

Several apple seedlings had been infected with spores from material resembling the second type mentioned above. A considerable number of aecidia matured. Spores from these aecidia were sowed on a red cedar, No. 418, in June, 1914. No infection was discovered on this cedar in 1915, but two sori developed on the main stem in May, 1916. In 1917, even on this small plant, the swollen sori coalesced in masses two inches long. The infection has spread over five inches vertically during the past three years. Old and new branches growing from the infected portion of the stem appear not to be infected at all. It is a typical trunk infection, and slightly fusiform. Amelanchier and Malus have been infected with spores from a single sorus two years in succession and there can be no doubt that both the shad bush and the apple are host plants for this form of G. nidus-avis.

Twelve red cedars were sprayed with spores from G. nidus-avis on Amelanchier in 1916. Only three of the plants have become infected, one of these in five different places. Cedar No. 414 was inoculated with spores from Amelanchier No. 878, June 11, 1916. Three small tongue-shaped sori were found among the young leaves of a side branch on April 5, 1917. This branch has since died. Cedar No. 929 had not been exposed to infection since 1913. The original teleutospore material with which the experiment was begun was obtained at Fort Lee, New Jersey, May 10, 1916. The infected branch, about two inches in diameter, had a very rough appearance and was covered with corky mounds and swellings. The sori when swollen were tremella-like and about an inch long. Amelanchier "canadensis" No. 878 was sprayed May 14. Spermogonia appeared on the leaves May 21, and aecidia were fully matured on the fruits June 9. Only a few aecidia developed on the leaves, although they had previously borne a great many spermogonia. No. 929 cedar was then sprayed with aecidiospores June 9; it was put in the cold frame October 22 and taken out March 7, 1917. A swelling and distortion of the main stem at the tip was plainly visible about November 1, although no sori had been noticed during the early months of spring. This plant was brought back to the green house again January 6, 1918. Sections of the swollen region were made January 17, 1918 and showed two annual rings of wood and two developing sori. No callus scars have been found on these sections, showing that a sorus had developed in 1917. In this case the resulting infection was just about of the type we should expect, and we can imagine it might have in years come to look much like the original infection with which we started. Photographs and specimens of all stages have been preserved.

The history of the infection of cedar No. 609 is more interesting. The teleutospore material was obtained from the largest infected red cedar on the grounds of the New York Botanical Garden. The trunk of this tree is heavily infected for a distance of several feet and has developed a large spindle-shaped swelling three feet long about ten feet above the ground. Amelanchier "canadensis" No. 886 was sprayed May 17, 1916. Spermogonia appeared May 26 and aecidia ripened on the fruit June 12. Red cedar No. 609

(six inches high June 6, 1915) was inoculated June 21, 1916. On March 22, 1917, twenty-one days after it had been taken from the cold frame, one very light-colored orange-yellow sorus developed in the axil of the leaf. This was supposed to be a sorus of G. clavipes that resulted from accidental infection in 1917. The little branch was marked with a tag. The plant was taken from the cold frame again January 7, 1918. On February 15, there were two light-colored sori in the axils of the leaves of the tagged branch. February 19 two more sori were discovered in the axils of leaves of another branch, and two strictly foliicolous sori on opposite leaves of another branch. March 5 another foliicolous sorus appeared on another branch, and at the base of a larger branch a small brown sorus was found, upon removing a piece of loose cork. All of the leaf sori were very light colored and looked like G. clavipes. The mycelium has been traced from the infected leaves down into the branches for about two centimeters. The infected branches are all on parts of the plant that have grown since it could have been exposed to natural infection. I have proved by the examination of spores, by sections of infected leaves and branches and by infection of the shad bush that this cedar was infected in 1916 with G. nidus-avis. Some of the infections appeared one year after inoculation, while it undoubtedly required two years for other sori to mature. This is the fourth species of Gymnosporangium which I have found requiring either one or two years in which to mature the teleutospores. Under favorable conditions the rust may develop in one year.

# GYMNOSPORANGIUM TRANSFORMANS AND G. FRATERNUM

Kern (8) describes G. fraternum as an annual species. The writer (3) called attention to the fact that there are two leaf forms of this genus on Chamaecyparis, both of which are frequently perennial, and in another paper (4) showed how the two forms could be distinguished by the character of the buffer cells that precede the teleutospores in the sori of each.

Blueprints were made of infected branches so that leaves bearing sori could be located on the prints. In many cases it was found that sori developed a second and third year on the same leaves. To prove that the species were distinct, spores from individual sori were germinated and smeared on selected leaves of both *Amelanchier* and *Aronia*. Slide mounts of the spores were then preserved and photographed. A few of the photographs are shown in Plate 8. Table VI, A and B, is arranged to show the effect of inoculating both trial hosts with spores from the same sorus.

TABLE VI

PARALLEL INOCULATIONS OF Amelanchier and Aronia with Individual Sori From LEAVES OF Chamaecyparis, 1916

A. G. fraternum

		,,,			
Date	Amelanchier	Result	Aronia	Result	Source of sorus
Feb. 22	49 I	+	642	-	435.3*
Ap. 18	558	+	806		721.1
Ap. 18	556	-	808 ,	_	721.10
Ap. 18	651	surerio	809	_	721.5
Ap. 18	807	+	344	-	721.8
Ap. 18	810	-	256	- man	721.4
Ap. 18	485	+	250	-	721.11
Ap. 20	820	+	818	-	721.3
Ap. 20	554	+	819	_	721.2
Ap. 20	821	+	822	· -	721.7
May 8	864	+ 1	456		746.1
May 8	484	+	470	[ -	746.2
	В	. G. transfe	rmans		
Feb. 22	441	- 1	465	-	435.2
Feb. 26	438c		452	+	423.I
Feb. 22	503		643	-	435.2
Feb. 26	552		452	+	423.2
Mch. I	553	- 1	454	+	424.2
Mch. 7	649	- !	518	+	400.2
Mch. 3	4304	- 1	645	-	424.I
Ap. 27	653	- 1	457	+	701.0
Ap. 7	653	- 1	652	_	437.1
Ap. 7	651	-	650		437.2
My. 10	654	-	808	+	710.1
3.45	0		9.06	1	H20 T

Referring to the table it can be seen under "A" that G. fraternum infected nine of the twelve amelanchiers inoculated, while the aronias were not infected. Under "B" where the thicker-walled teleutospores, G. transformans, were used seven Aronias were infected, five gave no results, and none of the amelanchiers was infected. In addition to the cultures shown in the table, 32 amelanchiers have been heavily infected by spraying with care-

My. 17

<sup>\*</sup> Means that the sorus used was sorus No. 3 from plant No. 435.

fully chosen sori of G. fraternum and 50 aronias with G. transformans without the infection of control plants used in either case.

So far as color, size and thickness of walls are concerned, one finds sori made up of intermediate types of spores not so easily identified. Compare Figs. 3 and 5 (*G. transformans*) with Fig. 7 (*G. fraternum*). On the contrary, such types as are shown in Fig. 6 (*G. transformans*) and Fig. 8 (*G. fraternum*) are easily distinguished. Spores of *G. biseptatum* are shown in Figs. 9 and 10 for comparison. *G. fraternum* does not become *G. biseptatum* when grown in the greenhouse.

## INFECTION OF CHAMAECYPARIS WITH G. TRANSFORMANS

The ninety-eight seedling plants of *Chamaecyparis* described in connection with cultures of *G. Ellisii* (Table IV, B) were used for this work. None of them developed rust in 1916. Most of them had no branches and only subulate leaves when brought in (1915). All new growth could be determined readily. Twenty-four plants were inoculated and seventy-four were kept in another greenhouse as controls. The results of these experiments are given in Table VII.

TABLE VII

INFECTION OF Chamdecyparis with G. transformans in 1916

No.	Dates of inoculation	Results, number of sori, March-April, 1917.	Controls
615	May 2, Aug. 28	5	Plants numbered 610-
617	June 1, Aug. 28	II	614, 616, 620, 625, 629,
618	June I, Aug. 28	2	790-798, 906, 908, 909,
619	July 16, Aug. 28	I	914-921, 948-958, 963-
621	June 1, Aug. 28	1	992, 1012, 1014-1016: re-
622	Apr. 24, Aug. 28	r	mained entirely free from
623	July 23, Aug. 28	5	this rust in 1917 and 1918
624	Apr. 24, Aug. 28	3	
626	Apr. 24, Aug. 28	2	
627	Apr. 24, Aug. 28	ı	
628	July 16, Aug. 28	12	
788	June 1, Aug. 28	Plant died.	
789	May 7, Aug. 28	0	
900	Apr. 26, Aug. 28	0	
901	Apr. 24, Aug. 28	' I	
902	Apr. 24, Aug. 28	21	
903	Apr. 24, Aug. 28	0	
904	Apr. 24, Aug. 28	r	
905	Apr. 24, Aug. 28	ı	
907	Aug. 28	0	
910	May 2, Aug. 28	0	
911	May 2, Aug. 28	II	
912	May 2, Aug. 28	Plant died.	
913	May 2, Aug. 28	0	

Sixteen of the twenty-four plants inoculated gave positive results, showing seventy-nine separate infections. Six plants were not infected, two died. The time required for the full development of this species is only nine or ten months.

The endeavor to infect *Chamaecyparis* with *G. fraternum* and *G. biseptatum* has not as yet resulted in success.

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#### Explanation of plate 8

The photographs of spores were made from sori used in making the inoculations reported in Table VI. Magnification, about 350.

#### GYMNOSPORANGIUM TRANSFORMANS

Fig. 1. A typical spore of this species showing a germ pore at the apex of each cell. The cell wall is comparatively thick.

Fig. 2. A three-celled spore, the lower cell showing two germ pores near the septum.

FIG. 3. A comparatively long spore of the type that is difficult to distinguish from such spores of *G. fraternum* as are shown in Fig. 7. The germ pore at the apex of the terminal cell, shown in Fig. 3, appears to be a very characteristic feature. Spores of *G. fraternum* frequently germinate at the apex but the germ pore is not plainly marked.

Fig. 4. Small spores comparatively short. Both cells of three of them have already germinated.

Fig. 5. A group of very thin-walled spores shaped very much like spores of G. fraternum. The three-celled spore shown is easily distinguished by its shape from the three-celled spores of G. biseptatum shown in Fig. 10.

Fig. 6. Large, broad, dark brown spores, none of which has germinated.

#### GYMNOSPORANGIUM FRATERNUM

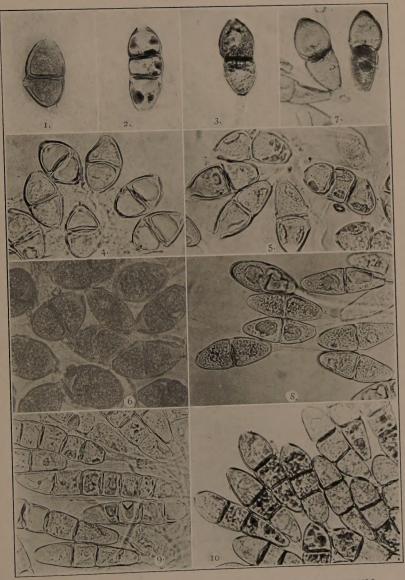
Fig. 7. Spores from a dark brown sorus. The spore wall of the upper cell is much thickened at the apex.

Fig. 8. Spores from a light rusty-orange-colored sorus. The pore at the apex of the upper cell is visible in one of the spores at the right. The spore walls are very thin.

#### GYMNOSPORANGIUM BISEPTATUM

Fig. 9. Spores from a sorus taken from the infection mentioned in another paper (Dodge, 4). This is the youngest infection I have been able to find in nature. The spores have from four to seven cells. There are very few three-celled spores.

Fig. 10. Spores from a sorus on a large burl about eight inches in length and two inches in diameter. Nearly every spore is three-celled.



DODGE: STUDIES IN THE GENUS GYMNOSPORANGIUM

